

## CRAB PREDATION ON LIMPETS: PREDATOR BEHAVIOR AND DEFENSIVE FEATURES OF THE SHELL MORPHOLOGY OF THE PREY<sup>1</sup>

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### ABSTRACT

The feeding behavior of rocky intertidal crabs in the tropical and temperate eastern Pacific was studied in relation to specific mechanical properties of the shells of their limpet prey. A series of laboratory experiments, involving direct observations, records of shell remains, and measurements of the forces generated by a feeding crab, showed that by far the most common feeding technique was to pry the margin of the limpet shell away from the substratum. The pattern of deformation in models of limpet shells subject to a similar prying force indicated (1) that the greatest stress on the shell was at the point of force application at the shell margin and (2) that the thickness of the shell margin contributed more to shell strength than did thickness in more apical regions of the shell. Measurements of the strength of real shells provided further support for this latter conclusion.

In addition, the strength of foot attachment, which sets the maximum prying force that the shell can experience, closely paralleled shell strength. This linkage between foot tenacity and shell strength appeared to be maintained via the degree of allometry between foot area and the thickness of the shell margin.

The potential for a particular predator feeding behavior to lead to selection for a defensive feature in shell morphology should be a function, not only of the frequency of occurrence of attacks, but also of the frequency of successful attacks. In particular, for selection to occur, some individuals must survive an attack so that they may pass on to their offspring the defensive feature that enabled survival. Compared to other crab feeding techniques, prying attacks on limpets occurred frequently and with low success. These data support the hypothesis that selection to resist prying forces has been an important feature in the evolution of limpet shell morphology.

### INTRODUCTION

Selection to resist attacks by shell-breaking predators appears to have been a central feature in the evolution of the shell form of marine gastropods (Vermeij, 1977; Vermeij *et al.*, 1980, 1981). Understanding of this selection pressure requires information on both the techniques of attack used by predators and the biomechanical properties of those parts of the shell that are most important in resisting these attacks. Previous studies of this kind have focused almost exclusively on gastropods with spirally coiled shells (Kitching *et al.*, 1966; Vermeij, 1974, 1976, 1978; Zipser and Vermeij, 1978; Palmer, 1979, 1985; Bertness and Cunningham, 1981). For these species, low spires, thickened shells, narrow or occluded apertures, and strong shell sculpture

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appear to reduce the probability of mortality due to attacks by shell-breaking predators such as fish and crustaceans. Very little information is available on those morphological attributes of gastropods with patelliform (limpet-shaped) shells that help to prevent predator-induced shell breakage (but see Chapin, 1968, and Lowell, 1985, 1986, 1987).

The three major groups of shell-breaking predators that feed on limpets are crabs (Chapin, 1968; R. B. Lowell, unpub. data), fish [only certain, mostly tropical, species generate shell-breaking forces before their limpet prey are detached from the substratum (Garrity and Levings, 1983; Lowell, 1987; S. D. Gaines, pers. comm.)], and birds (Feare, 1971; Hartwick, 1976, 1978, 1981; Frank, 1982; Hockey and Branch, 1983; Mercurio *et al.*, 1985) (see also Branch, 1981, for general review). Of these three groups, crabs (or other functionally similar decapods) are perhaps the most geographically and temporally ubiquitous in the rocky intertidal areas where limpets are found in the eastern Pacific (Ricketts and Calvin, 1968; Menge and Lubchenco, 1981; Frank, 1982; Lowell, 1986).

To determine the influence these crab predators may have had on the evolution of the shell form of rocky intertidal limpets, I recorded the techniques used by crabs to feed on limpets in the tropical and temperate eastern Pacific. The results of this study indicated that by far the most frequent feeding behavior was to attempt to pry the margin of the limpet's shell away from the substratum. Therefore, I measured the contribution of the characteristically thickened margin of the shell to the breaking resistance of the shells of several eastern Pacific limpet species which commonly co-occur with these crabs. I also determined the relationship between the breaking resistance of the shell and the attachment strength of the foot.

## MATERIALS AND METHODS

### *Crab feeding behavior*

*Temperate eastern Pacific.* Two species of cancrid crabs, *Cancer productus* and *C. oregonensis*, were chosen to study the feeding behavior of temperate Pacific crabs. Caging experiments have shown that these predatory crabs cause significant limpet mortality in the rocky intertidal; in addition, both species will readily attack limpets in the laboratory, often within seconds of being offered limpets for the first time (R. B. Lowell, unpub. data). *Cancer productus* attains fairly large sizes; the seven individuals (6 males, 1 female) used for this study ranged from 8.2 cm to 11.5 cm in maximum carapace width. *Cancer oregonensis* is a much smaller species; the two individuals (both female) used were 3.5 cm and 5.3 cm in maximum carapace width. No molts occurred during the study. All *C. productus* and one *C. oregonensis* were collected two years prior to the study from Bamfield Inlet (48°49'N, 125°8'W) and Grappler Inlet (48°50'N, 125°7'W) near the Bamfield Marine Station, British Columbia, Canada. The other, smaller *C. oregonensis* was collected from the plankton adjacent to the marine station at the postlarval (megalops) stage two years prior to the study and raised to maturity in the laboratory. All crabs were fed only bivalves (mostly *Mytilus edulis* and *Protothaca staminea*) and barnacles (mostly *Balanus glandula*) until 23 days before the first set of observations, after which they were fed only the four sets of limpets described below. Prior to the experimental period, each crab was placed in one of nine 37.5 l glass aquaria (50 × 25 × 30 cm) with a constant supply of fresh seawater. The crabs were then left undisturbed for 23 days before being offered the first set of limpets, except for two *C. productus* which were placed in their aquaria 1 day before being offered the first limpets. These latter two crabs

exhibited similar behavior to the other five *C. productus* throughout the study. To minimize disturbance, all aquaria were surrounded by black plastic sheets which admitted only dim light. The aquaria were situated in a room with a west-facing window. Although no attempt was made to regulate artificial lighting conditions exterior to the plastic enclosures, all crabs were most active during the late afternoon and through the night.

Four different size-shape classes of limpets were offered to each crab over a period of two months in 1984. To vary shape, the limpets were divided by species into a flat shell group (*Notoacmea scutum*) and a tall shell group (*Collisella pelta*, *N. persona*). To vary size, the limpets were further divided into small (18–23 mm in shell length) and large (30–40 mm) individuals. The four size-shape combinations were offered to the two crab species as follows: (1) five small, flat *N. scutum* per crab on 4 August; (2) four large, flat *N. scutum* per crab on 18 September; (3) five small, tall *C. pelta* per crab on 22 September; (4) four large, tall *N. persona* per crab on 24 September (*C. productus*) and 25 September (*C. oregonensis*). All crabs were offered each combination except that one *C. oregonensis* (3.5 cm) was not offered combination 4.

The limpets were collected one day before each of the observational trials from the following locations near the Bamfield Marine Station: small *N. scutum*—Kirby Point (48°51'N, 125°12'W); large *N. scutum* and *N. persona*—Ross Islets (48°52'N, 125°9'W); small *C. pelta*—Prasiola Point (48°49'N, 125°10'W). Four or five limpets were placed on each of nine flat rocks (upper surface area approximately 100 cm<sup>2</sup>). The following day, one rock was placed in each of the nine crab aquaria during the late afternoon and, in most cases, the feeding behavior of the crabs was observed for 40–95 minutes. Following these direct observations, the limpets were left with the crabs and their fates (alive vs. dead, shell whole vs. shell broken) were recorded at 2–24 hour intervals over the next 1–5 days. Shells with minor chips that did not extend beyond the thickened part of the shell margin (such chips would not expose the soft parts of a live, attached limpet) were not recorded as broken. At the beginning of each new trial, all limpets from the previous trial were removed.

Although not studied in detail, several measurements were made of the prying forces generated by a small crab while attempting to detach a limpet. A small (5.9 cm maximum carapace width) *C. productus* was collected in Grappler Inlet and held for several months in a shallow seawater tray (approximately 70 × 70 × 20 cm) connected to the same seawater system as used for the aquaria described above. Prior to the prying force measurements, this crab was fed a combination of bivalves (mostly *P. staminea*) and limpets (mostly *N. scutum*). Although artificial lighting conditions were not controlled, this crab was also most active at night.

To measure prying force, the shell of a newly killed *N. scutum* (30.6 mm in length) was tethered by a strand of nylon filament (glued into the interior apex of the shell) running through a sheet of Plexiglas to a force transducer. The force transducer, on the opposite side of the Plexiglas sheet from the tethered shell, was positioned so as to hold the shell (via the tether) against the sheet with a force of 2.7 N. The whole setup, with the plane of the Plexiglas sheet oriented vertically, was then placed in the seawater tray at 21:30 and left until 12:30 the following day. The prying forces generated by the crab were recorded throughout this period on a strip chart recorder; the crab's behavior was also observed for the first three hours.

*Tropical eastern Pacific.* The feeding behavior of five species of tropical Pacific xanthid crabs was studied at the Naos Laboratory of the Smithsonian Tropical Research Institute in Panama. Two of these species (*Ozius verreuxii*, *Eriphia squamata*) are the most common predatory crabs co-occurring on intertidal bedrock or boulders with the tropical limpets studied (Lubchenco *et al.*, 1984). The other three (*Eurypa-*



*nopen* (*Planus*, *Xanthodius sternburghii*, *Leptodius taboganus*) are more common on cobble beaches where these limpets, though present, are less common (J. H. Christy, R. B. Lowell, pers. obs.). All five species readily feed on limpets in the laboratory. Relative to *C. productus*, these crab species are all fairly small. The size ranges (maximum carapace width) and number of individuals used for each species were as follows: *O. verreuxii*—3.9–7.1 cm, 1 male, 3 females; *E. squamata*—3.0–4.5 cm, 3 males, 1 female; *E. planus*—2.1–2.3 cm, 3 males; *X. sternburghii*—2.8–3.1 cm, 10 males; *L. taboganus*—2.7 cm, 1 male. All crabs were collected from small islands (Naos, Culebra, 8°55'N, 79°32'W; Taboguilla, 8°48'N, 79°31'W) in the Bay of Panama (see Garrity and Levings, 1981, for descriptions of these islands) over several weeks prior to the observational trials.

The crabs were fed only the limpets used in these trials. For *O. verreuxii* and *E. squamata*, crabs were held individually, one in each of eight glass aquaria; individuals of each of the other three species were held together, one species in each of three glass aquaria. All aquaria (each approximately 12 l) were kept in outdoor tanks under transparent roofing where they received a constant supply of fresh seawater. No attempt was made to control artificial lighting conditions; nevertheless, the crabs were most active at night.

Three to four different size-classes (see Table V) of one limpet species (*Fissurella virescens*—tall shells) were introduced into each aquarium over a one month period (20 March–11 April 1984). Each size class was offered separately in increasing order starting with the smallest class. Although no attempt was made to standardize hunger levels, each trial was separated by at least four days. All limpets were collected from Culebra Island. The procedures for collecting the limpets and offering them to the crabs were the same as those for the temperate Pacific study.

### *Mechanical performance of the shell*

*Shell models.* All limpet species used in this study from both tropical and temperate shores exhibited characteristically thickened shell margins (R. B. Lowell, unpub. data). To determine the contribution of the thickened shell margin to the strength of the shell when subject to a crab-induced prying force, I sought to compare shells with a natural thickness distribution to shells that were identical in all respects except for being of constant thickness throughout all regions of the shell. Of the several thousand eastern Pacific limpet shells that were handled during the course of this and other related studies, I never found one to have a constant thickness distribution. Therefore, it was necessary to make this comparison by constructing naturally shaped models of limpet shells. By using a homogeneous material for these models, it was also possible to avoid differences in shell strength due to differences in the thicknesses of various shell microstructures (Currey, 1980).

These homogeneous models were composed of a "fiberglass" mixture of powdered glass embedded in Coating Resin P-18 which was hardened with Catalyst P-102 (Fiberlay, Inc., Seattle, Washington). I formed the models by using a silicone rubber cast of a real *N. scutum* shell (see Fig. 3 for the dimensions and thickness profile of this shell). Four models with a natural thickness distribution were formed from full casts. Three models with a constant thickness distribution (approximately 0.8 mm thick) were formed in the following manner. A positive cast, in the form of an epoxy plug, was made from the original negative cast of the dorsal surface of the shell. By using a micromanipulator to move the positive and negative casts away



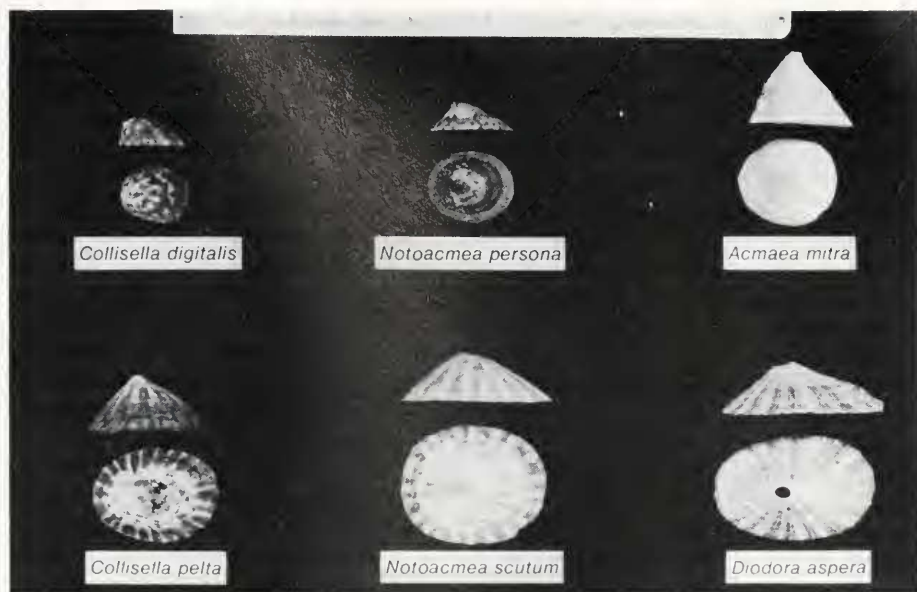


FIGURE 1. Lateral (top) and dorsal (bottom) views of temperate eastern Pacific limpet shells. Anterior side of shell faces left. 15 cm rule at top of figure.

from each other, it was possible to create an intervening space of any desired thickness which was of the same shape as the original shell. This space was filled with the "fiberglass" mixture to form the constant thickness models. The same amount of "fiberglass" was used to form both model types so that they differed only in their thickness profiles.

When a live limpet is subject to a crab-induced prying force, the force is transmitted from the shell to the foot (and, finally, to the substratum) via the horseshoe-shaped muscle scar where the foot muscle attaches to the shell. Therefore, I attached the shell models to fixed platforms with horseshoe-shaped strips of aluminum foil which were glued to the models along the ventral region of the model where this muscle scar would normally be found. A prying force, similar to that applied by a crab, was applied in a dorsal direction to the anterior margin of each model with a weighted 1.16 mm diameter steel hook of circular cross section.

To determine the patterns of deformation of the shell models, each model was coated with a spray-on brittle lacquer (Tens-Lac TL-500-75A with Undercoat U-10-A, Measurements Group, Charlotte, North Carolina). This lacquer cracks easily and the crack patterns are useful for determining the patterns of tensile strain (deformation) in a rigid structure which is subject to a force acting to deform the structure (Preuschoft *et al.*, 1975). The area where the lacquer first cracks indicates the area of greatest tensile strain. Since the shell models were made of a homogeneous material, the area of greatest strain would correspond to the area of greatest tensile stress (force/cross-sectional area). Mollusc shell material is much weaker in tension than in compression (Currey, 1980). Consequently, the area of greatest tensile stress is where the shell would most likely break.

*Shell strength and foot tenacity.* The strengths of various sides of the margins of real shells for several eastern Pacific limpet species also was measured. In the temper-

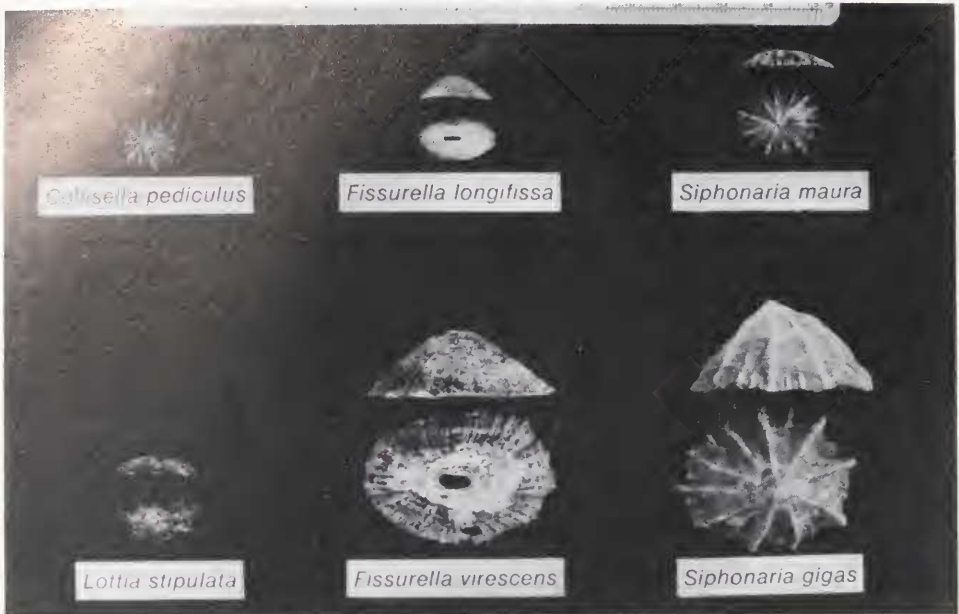


FIGURE 2. Lateral (top) and dorsal (bottom) views of tropical eastern Pacific limpet shells. See Figure 1 legend for further information.

ate eastern Pacific, measurements were taken for six common species from the west side of San Juan Island, Washington (Lime Kiln Lighthouse,  $48^{\circ}31'N$ ,  $123^{\circ}9'W$ ; False Bay,  $48^{\circ}29'N$ ,  $123^{\circ}4'W$ ): Acmaeidae—*Collisella digitalis*, *C. pelta*, *Notoacmea persona*, *N. scutum*, *Acmaea mitra*; Fissurellidae—*Diodora aspera* (Fig. 1). In the tropical eastern Pacific, measurements were taken for six additional common species from the south side of Taboguilla Island: Acmaeidae—*Collisella pediculus*, *Lottia (Scurria)*; Lindberg and McLean, 1981) *stipulata*; Fissurellidae—*Fissurella longifissa*, *F. virescens*; Siphonariidae—*Siphonaria gigas*, *S. maura* (Fig. 2).

To measure the strengths of these real limpet shells, I used a procedure similar to that used for the shell models. The shells of newly killed limpets were mounted, while still wet, onto one shaft of a Monsanto (type W) tensiometer. As for the shell models, a 1.16 mm diameter steel hook (in this case, attached to the other shaft of the tensiometer) subjected the edge of the shell to a prying force. The force required to break the shell was recorded. Hooks 0.67 mm and 2.64 mm in diameter were used for particularly small and large shells, respectively (Lowell, 1987); hook diameter had no significant effect on the force needed to break the shells (Lowell, 1985).

To mount the shells securely enough to withstand the force required to break the shell, it was necessary to provide a greater surface area for the glue to attach than the area of the muscle scar. Since the shell model experiment showed that the area of greatest stress in a shell subject to a prying force is at the point of force application at the margin of the shell (see Results), the real shells were mounted via two steel cables inserted into a pool of quick-setting epoxy put into the interior apical region of the shell dorsal to and overlapping the edges of the muscle scar. This method of mounting was double-checked by mounting lacquer-coated shell models (3 natural thickness, 4 constant thickness) in the same manner and subjecting them to prying forces. This

TABLE I

Regressions of foot length (FL, in mm) against shell length (SL, in mm) for eastern Pacific limpet species

Species	Equation	Range	n	r	P
<b>TEMPERATE</b>					
<i>Acmaea mitra</i>	FL = -2.13 + 0.755SL	10.5-33.5	12	0.9888	<0.0001
<i>Collisella digitalis</i>	FL = -1.61 + 0.743SL	11.8-25.2	10	0.9889	<0.0001
<i>Collisella pelta</i>	FL = 0.38 + 0.689SL	13.1-33.9	10	0.9865	<0.0001
<i>Notoacmea persona</i>	FL = -2.55 + 0.753SL	10.0-31.8	11	0.9958	<0.0001
<i>Notoacmea scutum</i>	FL = 1.07 + 0.612SL	23.1-49.7	11	0.9892	<0.0001
<i>Diodora aspera</i>	FL = 1.98 + 0.757SL	21.2-52.5	11	0.9648	<0.0001
<b>TROPICAL</b>					
<i>Collisella pediculus</i>	FL = 0.38 + 0.551SL	6.0-15.0	9	0.9318	0.0003
<i>Lottia stipulata</i>	FL = -2.13 + 0.761SL	13.3-21.1	10	0.9617	<0.0001
<i>Fissurella longifissa</i>	FL = 0.67 + 0.662SL	10.2-19.2	10	0.9808	<0.0001
<i>Fissurella virescens</i>	FL = -0.85 + 0.716SL	13.9-40.4	10	0.9863	<0.0001
<i>Siphonaria gigas</i>	FL = -2.33 + 0.748SL	8.7-48.1	12	0.9904	<0.0001
<i>Siphonaria maura</i>	FL = -1.80 + 0.905SL	10.4-18.7	10	0.9742	<0.0001

Range indicates maximum and minimum values for shell lengths used in regressions. n—sample size; r—correlation coefficient; P—probability that  $r = 0$ .

mounting procedure yielded the same results as those reported for the more natural procedure of mounting the models with strips of aluminum foil attached only to the region of the model where the muscle scar would normally be. The quick-setting epoxy generated heat while setting; to minimize any potential effects of this heating on the strength of the real shells, the dorsal surface of each shell was kept immersed in seawater while the epoxy was setting. All shells broke at the shell margin rather than around the apical region.

The maximum possible prying force that the margin of a limpet shell can experience is set by the maximum strength of attachment of the foot to the substratum (maximum tenacity). Therefore, one would expect selection for the strength of the shell margin to be sensitive to maximum tenacity (Lowell, 1985, 1987). I used spring scales to measure the maximum tenacity of previously undisturbed, healthy limpets on flat rock surfaces (except for two *S. gigas*, see below) in the field. These measurements were made by subjecting the margin of the shell to a prying force in a manner identical to and on the same sides of the shell as for the shell strength measurements. In addition, the limpets used in the tenacity measurements came from the same populations as those used in the shell strength measurements. On average, the Panamanian limpets attain much higher tenacities than the northeastern Pacific limpets (Lowell, 1987) and, possibly in consequence, the incidence of damage to the foot during detachment was much greater for the Panamanian limpets.

Both shell strength and foot tenacity were measured for limpets of a variety of different sizes. Foot area, estimated from measurements of shell length and width, was chosen as a measure of size because of its relevance to tenacity. Tenacity was always measured after the foot had tightly clamped to the substratum. Therefore, maximum foot length (FL) and width (FW) were measured for several individuals (collected from the same populations used for the shell strength and foot tenacity measurements) of each species while they were tightly clamped to transparent glass plates (FL for both *Siphonaria* species included the length of the ventral surface of the head, which was also used for adhesion by these two species). The relationship of shell length and width to foot length and width was then calculated (Tables I, II). Foot



TABLE II

Regression of foot width (FW, in mm) against shell width (SW, in mm) for eastern Pacific limpet species

Species	Equation	Range	n	r	P
<b>TEMPERATE</b>					
<i>Acmaea mitra</i>	FW = -1.30 + 0.795SW	8.7-28.8	12	0.9729	<0.0001
<i>Collisella digitalis</i>	FW = -1.33 + 0.750SW	8.5-20.1	10	0.9613	<0.0001
<i>Collisella pelta</i>	FW = 1.58 + 0.675SW	9.1-27.0	10	0.9827	<0.0001
<i>Notoacmea persona</i>	FW = -1.63 + 0.729SW	7.7-26.6	11	0.9878	<0.0001
<i>Notoacmea scutum</i>	FW = -1.29 + 0.761SW	17.8-39.5	11	0.9768	<0.0001
<i>Diodora aspera</i>	FW = -1.11 + 0.957SW	14.4-34.4	11	0.9530	<0.0001
<b>TROPICAL</b>					
<i>Collisella pediculus</i>	FW = -0.17 + 0.627SW	5.1-11.2	9	0.9455	0.0001
<i>Lottia stipulata</i>	FW = -0.99 + 0.795SW	9.5-15.6	10	0.9395	0.0001
<i>Fissurella longifissa</i>	FW = 0.94 + 0.641SW	6.5-11.1	10	0.9720	<0.0001
<i>Fissurella virescens</i>	FW = 0.99 + 0.622SW	9.1-29.1	10	0.9847	<0.0001
<i>Siphonaria gigas</i>	FW = -1.25 + 0.700SW	6.1-40.9	12	0.9976	<0.0001
<i>Siphonaria maura</i>	FW = 0.21 + 0.640SW	7.1-14.5	10	0.9556	<0.0001

Range indicates maximum and minimum values for shell widths used in regressions.

area (FA) was calculated as the area of an ellipse:  $FA = 0.25 \pi FL \cdot FW$  (Miller, 1974; Dimock, 1984).

One Panamanian species, *S. gigas*, is usually found on the backs of conspecifics when small. Therefore, the tenacities of the two smallest individuals used for this species were measured while on the backs of larger individuals. The two smallest *S. gigas* used for the shell strength measurements also came from the backs of larger individuals. Both the shell strengths and foot tenacities of these small *S. gigas* fell on the regression lines calculated for the larger *S. gigas*. Consequently, all sizes were pooled for the regressions given in Tables VI and VII.

**Statistics.** The limpets used in the following regression analyses were chosen so as to provide a fairly even distribution of sizes within the size ranges tested. In some cases, the data were log-transformed before analysis to linearize the data and homogenize the variances. For those analyses where neither the X nor Y variable could be regarded as the independent variable and where the regression equation was to be used for functional (slopes and intercepts to be compared among regressions) rather than predictive (regressions used merely to predict Y for a given X) purposes, the reduced major axis was calculated rather than the standard least squares regression line (Ricker, 1973, 1984).

## RESULTS

### Crab feeding behavior

**Direct observations.** The large temperate Pacific species, *C. productus*, exhibited four techniques for feeding on the limpets they were offered (Table III). (1) Pry—During this behavior, the tip of a chela or walking leg was inserted under the edge of a shell and an attempt was made to pry the shell away from the substratum. In most cases, the tip of the appendage was not fully under the edge of the shell and the attempt was unsuccessful. None of the crab species showed an obvious preference for a particular side of the shell. Rather, they usually probed around the edge of the shell until they found a sufficiently large space under the shell margin to initiate a prying

TABLE III

Direct observations of feeding techniques used by crabs

Crab species	Number of crabs	Limpet species	Limpet size (mm)	Dur obs	Feeding Technique												
					Prying			Lateral slide			Crush at apex			Crush at margins			
					U	S	%	U	S	%	U	S	%	U	S	%	
<i>Cancer productus</i>	7	<i>Notoacmea scutum</i> f	18-23	40	38	0	0	0	0	—	0	0	—	0	0	—	
<i>Cancer productus</i>	7	<i>Notoacmea scutum</i> f	30-40	95	82	0	0	0	0	—	0	0	—	0	0	—	
<i>Cancer productus</i>	7	<i>Collisella pelta</i> t	18-23	60	15	9	38	0	1	100	0	0	—	0	7	100	
<i>Cancer productus</i>	7	<i>Notoacmea persona</i> t	30-40	90	284	8	3	0	0	—	3	1	25	0	0	—	
					totals	419	17	4	0	1	100	3	1	25	0	7	100
<i>Cancer oregonensis</i>	2	<i>Notoacmea scutum</i> f	18-23	40	12	0	0	0	0	—	0	0	—	0	0	—	
<i>Cancer oregonensis</i>	2	<i>Notoacmea scutum</i> f	30-40	95	28	0	0	0	0	—	0	0	—	0	0	—	
<i>Cancer oregonensis</i>	2	<i>Collisella pelta</i> t	18-23	50	0	0	—	0	0	—	0	0	—	0	0	—	
					totals	40	0	0	0	0	—	0	0	—	0	0	—

Dur obs—duration of observations in minutes; U—number of unsuccessful attacks observed; S—number of successful attacks observed; %—percent successful attacks observed; f—flat, t—tall.

attack. All successful prying attacks which were directly observed resulted in the shell being detached whole. (2) Lateral slide—In one case, a *C. productus* successfully used its chela to slide a small, high-spired *C. pelta* off the rock in a lateral direction. (3) Crush at apex—Four attempts were made to crush the apex of large, tall *N. persona* between the two fingers of the chela. The apex of this species, though elevated, is rounded and provides a poor grip for an attacking crab; only one attempt was successful. (4) Crush at margins—Seven attempts by *C. productus* were made to crush the shells of small, steep-sided *C. pelta* between the fingers of one chela where each finger was placed at opposite margins of the shell. This technique was always immediately successful. The prying technique was by far the most common feeding behavior observed for *C. productus* (prying vs. all other techniques,  $\chi^2 = 441$ ,  $df = 1$ ,  $P < 0.0001$ ).

This latter tendency was even more pronounced for the smaller crab species. The prying technique was the only behavior observed for *C. oregonensis* (Table III). The Panamanian crabs were more reluctant to feed while being observed and direct observations of their feeding behavior were not quantified. Nevertheless, of more than fifty observed attacks by *O. verreuxii* and *E. squamata*, only the prying technique was seen.

*Shell remains.* The high frequency of prying attacks also may be inferred from the high frequency of whole shells that were found during 1–8 days of feeding (Tables IV, V). The only other observed feeding behavior which resulted in shells being removed whole, the lateral sliding technique, was very rare (Table III). Since all crab species frequently broke up limpet shells after they were removed, most of the % whole values less than 100 in Tables IV and V probably greatly underestimate the frequency of successful prying attacks relative to other types of attacks. The shells of all or most of the limpets killed by the smallest crabs (*C. oregonensis*, *E. planus*, *X. sternburghii*, *L. taboganus*) were removed whole. The relative frequency of whole versus broken shells increased with increasing limpet size for the other crab species, although one comparison was not significant: *C. productus*—flat limpets (*N. scutum*), shell condition (whole or broken) vs. size,  $\chi^2 = 6.75$ ,  $df = 1$ ,  $P = 0.0094$ ; *C. produc-*

TABLE IV

Cona: ~~W~~ (whole vs. broken) of shells of limpets offered to temperate crabs

Crab species	Number of crabs	Limpet species	Limpet size (mm)	Dur obs	Whole	Broken	Alive	% Whole
<i>Cancer productus</i>	7	<i>Notoacmea scutum</i> f	18-23	2	0	11	24	0
<i>Cancer productus</i>	7	<i>Notoacmea scutum</i> f	30-40	3	8	10	10	44
<i>Cancer productus</i>	7	<i>Collisella pelta</i> t	18-23	1	13	22	0	37
<i>Cancer productus</i>	7	<i>Notoacmea persona</i> t	30-40	1	14	10	4	58
<i>Cancer oregonensis</i>	2	<i>Notoacmea scutum</i> f	18-23	2	4	1	5	80
<i>Cancer oregonensis</i>	2	<i>Notoacmea scutum</i> f	30-40	3	6	1	1	86
<i>Cancer oregonensis</i>	2	<i>Collisella pelta</i> t	18-23	4	10	0	0	100
<i>Cancer oregonensis</i>	1	<i>Notoacmea persona</i> t	30-40	5	4	0	0	100

Dur obs—Duration of observations in days; Whole—number of shells known to be detached whole; Broken—number of shells broken either during or after detachment; Alive—number of limpets alive at end of feeding trial; % Whole—percent known to be detached whole of those eaten; f—flat, t—tall.

tus—tall limpets (*C. pelta*, *N. persona*), shell condition vs. size,  $\chi^2 = 2.58$ ,  $df = 1$ ,  $P = 0.109$ ; *O. verreuxii*—*F. virescens*, % whole vs. size (Spearman's Rank Correlation),  $r = 0.8531$ ,  $n = 12$ ,  $P = 0.0047$ ; *E. squamata*—*F. virescens*, % whole vs. size (Spearman's Rank Correlation),  $r = 0.7937$ ,  $n = 12$ ,  $P = 0.0085$ . Most of the increased frequency of whole shells observed for the larger limpets was probably due to decreased breakage while manipulating the shell after being removed. Some of this increase in whole shell frequency, however, was probably also due to an increase in prying attacks as the ratio of limpet size to crab size increased.

TABLE V

Condition (whole vs. broken) of shells of *Fissurella virescens* offered to tropical crabs

Crab species	Number of crabs	Limpet size (mm)	Dur obs	Whole	Broken	Alive	% Whole
<i>Ozius verreuxii</i>	4	15-20	1	3	14	3	18
<i>Ozius verreuxii</i>	4	25-30	1	13	5	2	72
<i>Ozius verreuxii</i>	3	35-40	1	11	0	2	100
<i>Ozius verreuxii</i>	1	40-45	1	3	0	0	100
<i>Eriphia squamata</i>	4	15-20	1	1	17	2	6
<i>Eriphia squamata</i>	4	25-30	1	9	3	8	75
<i>Eriphia squamata</i>	4	35-40	1	5	1	10	83
<i>Eurypanopeus planus</i>	3	15-20	6	3	0	2	100
<i>Eurypanopeus planus</i>	3	20-30	6	3	0	2	100
<i>Eurypanopeus planus</i>	3	35-40	1	1	0	3	100
<i>Xanthodius sternburghii</i>	10	15-20	6	2	0	3	100
<i>Xanthodius sternburghii</i>	10	20-30	6	3	0	2	100
<i>Xanthodius sternburghii</i>	10	35-40	1	2	0	2	100
<i>Leptodius taboganus</i>	1	15-20	8	1	0	4	100
<i>Leptodius taboganus</i>	1	20-30	8	1	0	3	100
<i>Leptodius taboganus</i>	1	35-40	4	1	0	3	100

See Table IV legend for further information.



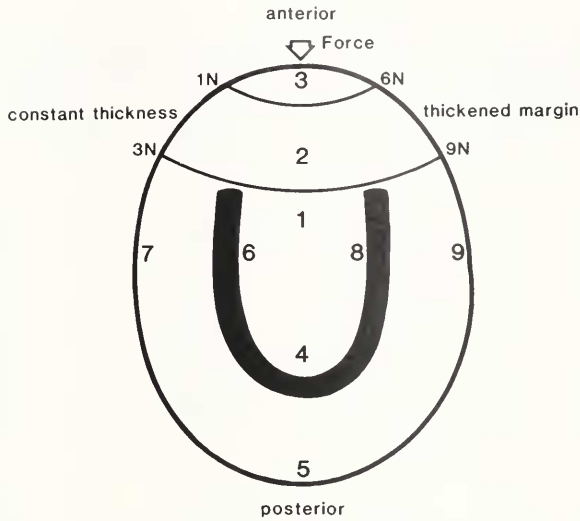


FIGURE 3. Diagrammatic ventral view of interior of shell model. The thin semicircular lines show the extent of deformation (as indicated by cracks in the brittle lacquer) at two levels of loading at the anterior edge of the model (arrow indicates where force applied; direction of force is into plane of figure). The values on the left are the forces that were required to deform the constant thickness models to the indicated radial distances from the point of force application. Those on the right are the forces required to deform the thickened margin models a similar amount. The shaded, horseshoe-shaped region shows approximately where the foot muscle would attach to the shell. Numerals 1–9 indicate the locations where shell thickness was measured on the *Notoacmea scutum* shell used to make the models. Location 1 was the apex. Locations 2, 4, 6, and 8 were in the thin annular region surrounding the apex. Locations 3, 5, 7, and 9 were at the thickest part of the shell margin. Thicknesses: 1—0.67 mm, 2—0.35 mm, 3—1.23 mm, 4—0.50 mm, 5—1.10 mm, 6—0.57 mm, 7—1.31 mm, 8—0.53 mm, 9—1.38 mm. Dimensions of whole shell: length—38.7 mm, width—31.7 mm, height—11.5 mm.

*Prying force.* Since no other food was available, the small *C. productus* used for the prying force measurements spent most of the night (22:30–09:30) attempting to pry the tethered shell away from the Plexiglas sheet. During this period, 610 separate prying forces were recorded. Most were 1–5 s in duration, although a few lasted up to 20 s. The peak force recorded was 10.1 N. The prying forces were generated with the tips of the walking legs or chelae and all sides of the shell were attacked. This left a record of tiny chips around the entire margin of the shell, although the thickened part of the margin remained intact.

#### *Mechanical performance of the shell*

*Shell models.* As the prying force was increased, the lacquer coating of all shell models first cracked on the ventral side of the shell at the point of force application. As the force was further increased, semicircular cracks formed farther from this point, creating the same concentric pattern on all models (Fig. 3). This indicates that the greatest stress was at the point of force application. In a detailed study of scallop shells subject to point forces, Pennington and Currey (1984) also measured a tendency for shell deformation to be greater near the point of force application.

Figure 3 also shows, for the two thickness distributions, the approximate force required to form cracks out to the indicated radial distances from the point of force application. The absolute magnitudes of these forces are unimportant since they are

TABLE VI

Equations for shell strength ( $F$ , in newtons) as a function of foot area ( $FA$ , in  $cm^2$ ) for all species and sides of shell

Species	Side	Equation	Range	n	r	P
<b>TEMPERATE</b>						
<i>Acmaea mitra</i>	A	$F = 54.4FA^{0.58}$	0.34–2.50	11	0.8131	0.0023
<i>Collisella digitalis</i>	A	$F = 42.3FA^{0.83}$	0.28–1.80	12	0.7769	0.0030
<i>Collisella digitalis</i>	P	$F = 33.2FA^{1.00}$	0.29–1.78	8	0.9231	0.0011
<i>Collisella pelta</i>	A	$F = 11.8FA^{1.31}$	1.18–4.35	11	0.7948	0.0035
<i>Collisella pelta</i>	R	$F = 13.6FA^{1.13}$	0.73–4.22	8	0.9709	0.0001
<i>Collisella pelta</i>	P	$F = 10.1FA^{1.28}$	0.80–3.34	7	0.9501	0.0010
<i>Notoacmea persona</i>	A	$F = 27.5FA^{0.63}$	0.19–2.95	8	0.8452	0.0012
<i>Notoacmea scutum</i>	A	$F = 11.6FA^{0.94}$	0.76–8.04	20	0.9091	<0.0001
<i>Notoacmea scutum</i>	R	$F = 13.0FA^{0.98}$	1.10–4.30	8	0.9077	0.0018
<i>Notoacmea scutum</i>	P	$F = 9.0FA^{1.10}$	1.19–5.91	8	0.9652	0.0001
<i>Diodora aspera</i>	A	$F = 14.0FA^{0.71}$	1.80–8.23	8	0.9180	0.0013
<b>TROPICAL</b>						
<i>Collisella pediculus</i>	A	$F = 76.5FA^{0.82}$	0.20–0.74	11	0.8306	0.0015
<i>Lottia stipulata</i>	A	$F = 28.6FA^{0.79}$	0.41–1.49	12	0.7654	0.0037
<i>Fissurella longifissa</i>	A	$F = 45.3FA^{1.53}$	0.37–1.65	12	0.9560	<0.0001
<i>Fissurella virescens</i>	A	$F = 40.1FA^{1.16}$	0.25–4.13	12	0.9815	<0.0001
<i>Fissurella virescens</i>	R	$F = 58.4FA^{0.91}$	0.34–6.37	12	0.9546	<0.0001
<i>Fissurella virescens</i>	P	$F = 47.0FA^{1.25}$	0.21–4.19	12	0.9813	<0.0001
<i>Siphonaria gigas</i>	A	$F = 62.0FA^{0.90}$	0.10–6.77	11	0.9873	<0.0001
<i>Siphonaria maura</i>	A	$F = 36.3FA^{1.10}$	0.53–1.58	9	0.7845	0.0123

Equations detransformed from linear regressions of  $\ln F$  vs.  $\ln FA$  ( $r$  and  $P$  values given for  $\ln$ - $\ln$  regressions). Range indicates maximum and minimum values for foot areas used in regressions. Side: A—anterior, R—right, P—posterior.

specific to the artificial material used for the models. Of significance is the result that much greater forces were required to cause a given degree of deformation or stress for the natural, thickened margin models as compared to the constant thickness models. Since the total amount of material used in each model type was equal, the constant thickness models had thicker apical regions and thinner shell margins than the natural thickness models. Therefore, these results indicate that, with respect to the strength of the shell when resisting prying forces, marginal thickness is of more importance than is thickness in more apical regions of the shell.

*Shell strength and foot tenacity.* For each species and side of the shell tested, the natural logarithm ( $\ln$ ) of the force required to break the shell (shell strength) and  $\ln$  of the force required to detach the foot (foot tenacity) were regressed against  $\ln$  foot area. In all cases, shell strength and foot tenacity showed a highly significant increase with increasing size (Tables VI, VII).

## DISCUSSION

### Crab feeding behavior

Three major patterns were evident in the results of the feeding experiments. First, the prying technique was clearly the most frequently observed feeding behavior for all limpets, including the seven *C. productus* and one *C. oregonensis* which had not fed on limpets for at least two years. Furthermore, the other *C. oregonensis*, which had been collected from the plankton, had never fed on limpets and was only observed

TABLE VII

Equations for foot tenacity ( $F$ , in newtons) as a function of foot area ( $FA$ , in  $cm^2$ ) for all species and sides of shell

Species	Side	Equation	Range	n	r	P
<b>TEMPERATE</b>						
<i>Acmaea mitra</i>	A	$F = 26.4FA^{0.77}$	0.25–4.29	10	0.9742	<0.0001
<i>Collisella digitalis</i>	A	$F = 21.9FA^{0.89}$	0.25–2.97	9	0.9782	<0.0001
<i>Collisella digitalis</i>	P	$F = 23.3FA^{0.85}$	0.32–1.52	8	0.8839	0.0036
<i>Collisella pelta</i>	A	$F = 7.6FA^{1.29}$	0.69–3.89	20	0.9278	<0.0001
<i>Collisella pelta</i>	R	$F = 8.8FA^{1.50}$	0.82–3.71	8	0.9600	0.0002
<i>Collisella pelta</i>	P	$F = 9.6FA^{1.57}$	0.91–3.36	8	0.9902	<0.0001
<i>Notoacmea persona</i>	A	$F = 21.1FA^{0.96}$	0.59–3.26	8	0.9945	<0.0001
<i>Notoacmea scutum</i>	A	$F = 8.1FA^{1.08}$	0.32–5.93	23	0.9662	<0.0001
<i>Notoacmea scutum</i>	R	$F = 12.9FA^{0.90}$	0.64–5.98	10	0.9215	0.0002
<i>Notoacmea scutum</i>	P	$F = 12.6FA^{0.92}$	0.90–5.46	8	0.9524	0.0003
<i>Diodora aspera</i>	A	$F = 7.4FA^{0.97}$	1.45–9.20	12	0.8841	0.0001
<b>TROPICAL</b>						
<i>Collisella pediculus</i>	A	$F = 27.8FA^{0.94}$	0.17–0.73	13	0.7673	0.0022
<i>Lottia stipitata</i>	A	$F = 26.0FA^{0.86}$	0.36–2.06	12	0.9652	<0.0001
<i>Fissurella longifissa</i>	A	$F = 41.4FA^{1.38}$	0.48–1.01	8	0.8913	0.0030
<i>Fissurella virescens</i>	A	$F = 33.1FA^{1.05}$	0.49–4.23	14	0.9571	<0.0001
<i>Fissurella virescens</i>	R	$F = 31.8FA^{1.07}$	0.39–3.26	9	0.9669	<0.0001
<i>Fissurella virescens</i>	P	$F = 33.4FA^{0.93}$	0.62–3.37	11	0.9806	<0.0001
<i>Siphonaria gigas</i>	A	$F = 32.9FA^{1.03}$	0.09–4.87	11	0.9834	<0.0001
<i>Siphonaria maura</i>	A	$F = 25.7FA^{1.06}$	0.42–2.00	10	0.9208	0.0002

See Table VI legend for further information.

to use the prying technique. These results indicate that the initial preference for prying attacks is not learned. Moreover, this pattern was maintained through two months of being fed only limpets, indicating that learning does not greatly change the strong preference for prying attacks (see Hughes, 1980, Lawton and Hughes, 1985, and references therein for discussions of the role of learning in the feeding behavior of crabs).

A second pattern observed was the increase in the relative frequency of prying attacks as the ratio of limpet size to crab size increased. When the ratio of limpet size to crab size is large, some of the other possible techniques (*e.g.*, crush at margins) become physically impossible. Other techniques become very difficult (*e.g.*, apex crush). In contrast, even small crabs can pry off large limpets if the limpet is caught before it has clamped down. This also should be true for lateral sliding attacks and the reason for the low frequency of this behavior is unknown. This low frequency may be related to the tendency for the edge of the shell to dig into the substratum when it is slid sideways. Undoubtedly, the prying forces generated by crabs include a lateral, in addition to a vertical, component. A switch in feeding behavior as the ratio of gastropod size to crab size increases has also been observed for crabs feeding on spirally coiled marine gastropods (Bertness and Cunningham, 1981; Reimchen, 1982; ap Rheinallt and Hughes, 1985; Lawton and Hughes, 1985).

A third pattern emerging from these observations was an increase in the relative frequency of prying attacks for flat shells as opposed to tall shells. This was probably due to the difficulty of attaining a purchase on flat shells for non-prying attacks.

In addition to differences in the frequency of occurrence of attacks, the various feeding techniques also differed in the frequency of success (Table III). The potential



TABLE VIII

Correlation matrix among thicknesses at several locations (1-7) on the shells of *Notoacmea scutum*

	1	2	3	4	5	6	7
1	1.0000						
2	0.8043	1.0000					
3	0.4973	0.7444	1.0000				
4	0.7716	0.8838	0.5636	1.0000			
5	0.5288	0.7973	0.9642	0.6373	1.0000		
6	0.7397	0.9072	0.6867	0.9081	0.7562	1.0000	
7	0.5582	0.7938	0.9599	0.6595	0.9680	0.7568	1.0000

n = 20 for all correlations. See Figure 3 for positions of locations.

for selection for defensive features of shell morphology is a function of both of these factors (Vermeij, 1985). For example, this point was illustrated in the one case where the crabs were large enough and the limpets small enough and of the right shape to enable the marginal crushing technique (*C. productus*—*C. pelta*). Combining all the attack techniques used in this case, over half the observed attacks were immediately successful (17 successful vs. 15 unsuccessful; Table III) and all limpets were eaten within four hours. For selection to favor a particular defensive feature of morphology, individuals possessing that feature must possess a higher probability of successfully surviving an attack than those lacking that feature. If the probability of surviving a series of attacks is vanishingly small regardless of morphology (as seems to be the case for marginal crushing attacks), selection is unlikely to occur (see Reimchen, 1980; Vermeij, 1982, 1985; Sih, 1985, for further discussion). The much higher probability of surviving a prying attack (Table III), coupled with the high frequency of this behavior, suggests that selection for morphological features of the shell which enhance resistance to prying forces is quite strong.

#### Mechanical performance of the shell

The results from the crab-behavior and the limpet-shell-model experiments emphasize the importance of the marginal thickness of limpet shells as a morphological

TABLE IX

Equations for shell strength ( $F$ , in newtons) as a function of shell thickness ( $T$ , in mm) at seven locations on the shells of *Notoacmea scutum*

Location	Equation	Range	r	P
1	$F = 57.3T^{1.00}$	0.23-1.50	0.6581	0.0016
2	$F = 160.3T^{1.45}$	0.15-0.66	0.7704	0.0001
3	$F = 44.6T^{1.39}$	0.31-1.57	0.8966	<0.0001
4	$F = 83.5T^{1.18}$	0.20-1.04	0.7030	0.0005
5	$F = 35.4T^{1.38}$	0.33-1.94	0.9054	<0.0001
6	$F = 92.1T^{1.26}$	0.20-1.07	0.7460	0.0002
7	$F = 35.2T^{1.53}$	0.39-1.72	0.9260	<0.0001

See Figure 3 for positions of locations. Equations detransformed from linear regressions of  $\ln F$  vs.  $\ln T$  (r and P values given for  $\ln$ - $\ln$  regressions). Range indicates maximum and minimum values for shell thicknesses used in regressions. n = 20 for all equations.

TABLE X

Equations for thickness at margin of shell ( $T$ , in mm) as a function of foot area ( $FA$ , in  $cm^2$ ) for all species and sides of shell

Species	Side	Equation	Range	n	r	P
<b>TEMPERATE</b>						
<i>Acmaea mitra</i>	A	$T = 1.03FA^{0.43}$	0.34–3.84	16	0.9221	<0.0001
<i>Collisella digitalis</i>	A	$T = 0.67FA^{0.63}$	0.28–1.80	24	0.8153	<0.0001
<i>Collisella digitalis</i>	P	$T = 1.04FA^{0.56}$	0.28–1.80	24	0.8939	<0.0001
<i>Collisella pelta</i>	A	$T = 0.37FA^{0.78*}$	0.69–4.55	88	0.8263	<0.0001
<i>Collisella pelta</i>	R	$T = 0.45FA^{0.73*}$	0.69–4.55	88	0.8765	<0.0001
<i>Collisella pelta</i>	P	$T = 0.44FA^{0.75*}$	0.69–4.55	88	0.8875	<0.0001
<i>Notoacmea persona</i>	A	$T = 0.57FA^{0.36}$	0.19–2.95	8	0.8940	0.0027
<i>Notoacmea scutum</i>	A	$T = 0.40FA^{0.66*}$	0.59–8.04	106	0.9180	<0.0001
<i>Notoacmea scutum</i>	R	$T = 0.48FA^{0.63*}$	0.59–8.04	106	0.9239	<0.0001
<i>Notoacmea scutum</i>	P	$T = 0.46FA^{0.68*}$	0.59–8.04	106	0.9234	<0.0001
<i>Diodora aspera</i>	A	$T = 0.51FA^{0.65*}$	1.80–8.23	8	0.9752	<0.0001
<b>TROPICAL</b>						
<i>Collisella pediculus</i>	A	$T = 1.47FA^{0.59}$	0.16–0.80	19	0.8702	<0.0001
<i>Lottia stipulata</i>	A	$T = 0.79FA^{0.49}$	0.41–1.49	15	0.7491	0.0013
<i>Fissurella longifissa</i>	A	$T = 0.94FA^{0.70*}$	0.30–1.65	13	0.9763	<0.0001
<i>Fissurella virescens</i>	A	$T = 0.93FA^{0.52}$	0.21–6.37	43	0.9604	<0.0001
<i>Fissurella virescens</i>	R	$T = 1.12FA^{0.55*}$	0.21–6.37	43	0.9702	<0.0001
<i>Fissurella virescens</i>	P	$T = 0.99FA^{0.58*}$	0.21–6.37	43	0.9613	<0.0001
<i>Siphonaria gigas</i>	A	$T = 1.29FA^{0.43*}$	0.10–7.26	16	0.9720	<0.0001
<i>Siphonaria maura</i>	A	$T = 0.85FA^{0.79*}$	0.31–1.58	16	0.7296	0.0013

Equations detransformed from linear regressions (reduced major axis) of  $\ln T$  vs.  $\ln FA$  ( $r$  and  $P$  values given for  $\ln$ - $\ln$  regressions). Range indicates maximum and minimum values for foot areas used in regressions. Side: A—anterior, R—right, P—posterior. \*—indicates significant ( $P < 0.05$ ) allometric increase or decrease of marginal thickness with increasing foot area, as indicated by an exponent that is significantly greater or less than 0.5. See Clarke, 1980, for significance tests for slopes of reduced major axis regressions.

defense against crab predation. This conclusion is further supported by the results of the strength measurements for real shells. For the strength measurements of the anterior side of *N. scutum*, thickness measurements at several locations on the shell were taken before the shells were broken. These locations corresponded to locations 1–7 of Figure 3 and included three positions along the shell margin and four positions in the apical region. Due to the high correlations between these thickness measurements, particularly between the measurements of marginal thickness (Table VIII), it was not feasible to analyze the relationship between shell strength and thickness using a single multiple regression (Bendel, 1971). Therefore, shell strength was instead regressed separately against each measure of shell thickness. The correlation coefficients for these regressions indicate that marginal thickness accounted for more of the variation in the strength of these real shells than did any of the apical thicknesses (Table IX).

The importance of marginal thickness to the strength of real limpet shells was further emphasized by comparisons among all the species tested. As for shell strength, marginal thickness also showed a highly significant increase with increasing size for all species and sides of the shell measured (Table X). These thickness measurements corresponded to the same sides of the shell for which shell strength and foot tenacity were measured. The measurements were made on the individuals used for the shell strength measurements (before breaking) and were supplemented with measure-

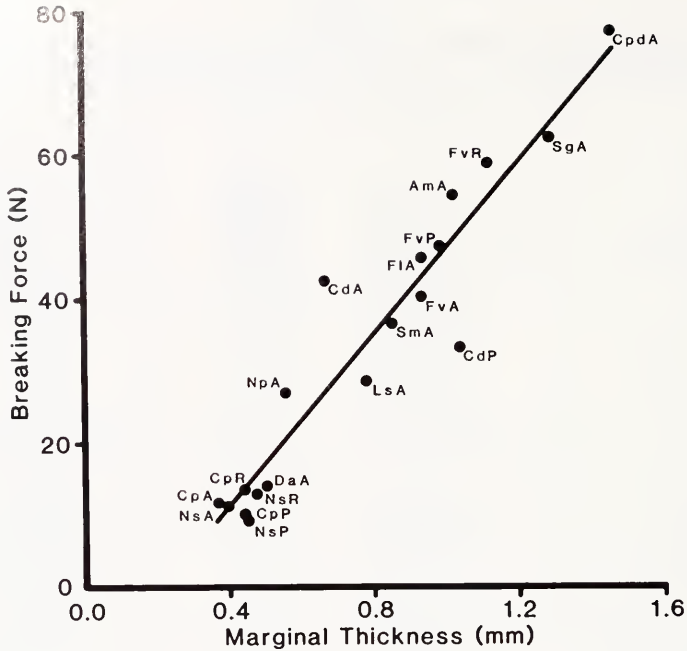


FIGURE 4. Force to break shell ( $F$ , in newtons) versus marginal thickness ( $T$ , in mm) at intermediate size (foot area =  $1 \text{ cm}^2$ ) for all species and sides of shell. Values calculated from equations in Tables VI and X. The regression line indicates the significant increase of shell strength with increasing marginal thickness:  $F = -12.6 + 59.1T$ ;  $n = 19$ ;  $r = 0.9517$ ,  $P < 0.0001$ . Temperate limpets: Am, *Acmaea mitra*; Cd, *Collisella digitalis*; Cp, *C. pelta*; Da, *Diodora aspera*; Np, *Notoacmea persona*; Ns, *N. scutum*. Tropical limpets: Cpd, *Collisella pediculus*; Fl, *Fissurella longifissa*; Fv, *F. virescens*; Ls, *Lottia stipulata*; Sg, *Siphonaria gigas*; Sm, *S. maura*. Sides of shell: A, anterior; R, right; P, posterior.

ments made on additional individuals from the same populations. For those species with radial ribs extending to the shell margin, thickness was calculated as the average of the rib and adjoining furrow thicknesses.

These ln-ln regressions (Tables VI, X) were then used to calculate shell strength and marginal thickness for each species and side of the shell at a single intermediate size (foot area =  $1 \text{ cm}^2$ ) common to all species. These two sets of measurements were regressed against each other and shell strength showed a highly significant increase with increasing marginal thickness (Fig. 4).

The prying forces exerted by crab predators on limpet shells differ from the breaking forces exerted by crabs on the shells of spirally coiled gastropods in that the maximum possible prying force on a limpet shell is set by foot tenacity (Lowell, 1985, 1987). This intrinsic limit does not apply to spirally coiled gastropods, the shells of which still provide protection from predators even after the foot is detached. Therefore, limpets are unique in that one would expect selection to act to link the mechanical performances of the shell and the foot, given a cost to excessively strengthening the shell (Palmer, 1981). This linkage has been demonstrated in interspecific comparisons of limpets in the eastern Pacific (Lowell, 1987).

Further, intraspecific evidence for the linkage of the performances of the shell and foot is evident in comparisons of the slope of ln shell strength regressed against ln foot area to the slope of ln foot tenacity regressed against ln foot area for each species



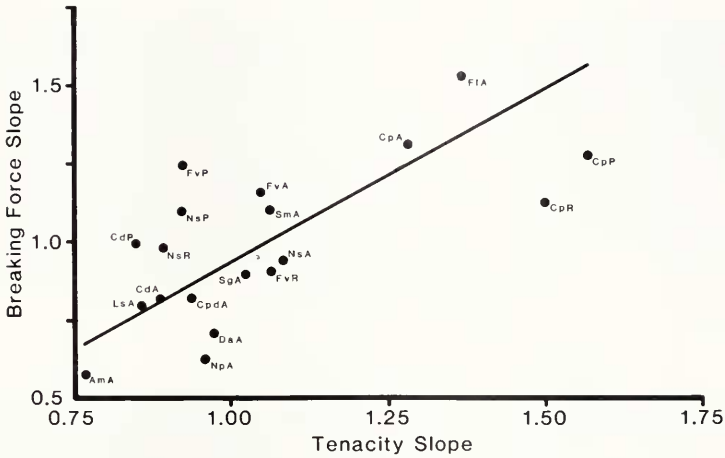


FIGURE 5. Slopes of shell strength ln-ln regressions (SS) versus slopes of foot tenacity ln-ln regressions (FT) for all species and sides of shell. Slopes given as exponents in Tables VI and VII. The regression line (reduced major axis) indicates a significant tendency for greater slopes for shell strength to be associated with greater slopes for foot tenacity:  $SS = -0.18 + 1.11FT$ ;  $n = 19$ ;  $r = 0.6708$ ;  $P = 0.0017$ . See Figure 4 for abbreviations.

and side of the shell tested (slopes given in detransformed form as exponents; Tables VI, VII). These two slopes differed significantly in only one of nineteen cases (*F. virescens*—posterior side; Lowell, 1987). This means that, for the most part, the shell strength and foot tenacity ln-ln regressions were essentially parallel. Thus, the ratio of shell strength to foot tenacity remained fairly constant with increasing size. This linkage between shell strength and foot tenacity over a wide range of different slopes is further emphasized by the highly significant correlation between the slopes for shell strength and those for foot tenacity for all species and sides of the shell combined (Fig. 5).

The linkage between shell strength and foot tenacity appears to be at least partially due to the degree of allometric increase of marginal thickness with increasing size. For an isometrically growing limpet, marginal thickness should increase as the square root of foot area due to simple geometric considerations. Several exponents in Table X were significantly different than 0.5, indicating an allometric change in marginal thickness with increasing foot area. Furthermore, the exponents in Table X (indicating degree of allometry) were highly correlated with the exponents for shell strength as a function of foot area in Table VI (Fig. 6). In other words, the rate of increase of shell strength with increasing size appears to be linked to the rate of increase of marginal thickness with increasing size. This suggests that the limpets can control shell strength so that it parallels foot tenacity by controlling the degree of allometry in marginal thickness.

Taken as a whole, these data underscore the relationship between the localized forces generated by crabs feeding on limpets and the localized thickening (= strengthening) of a specific region of the limpet shell, the shell margin. The strengths of whole shells have also been reported for a few species of bivalves (Elner, 1978; Currey, 1979; Blundon and Kennedy, 1982; Boulding, 1984) and spirally coiled gastropods (Currey, 1979; Vermeij and Currey, 1980; Currey and Hughes, 1982; Blundon and Vermeij, 1983). These measurements were all made by crushing whole shells between

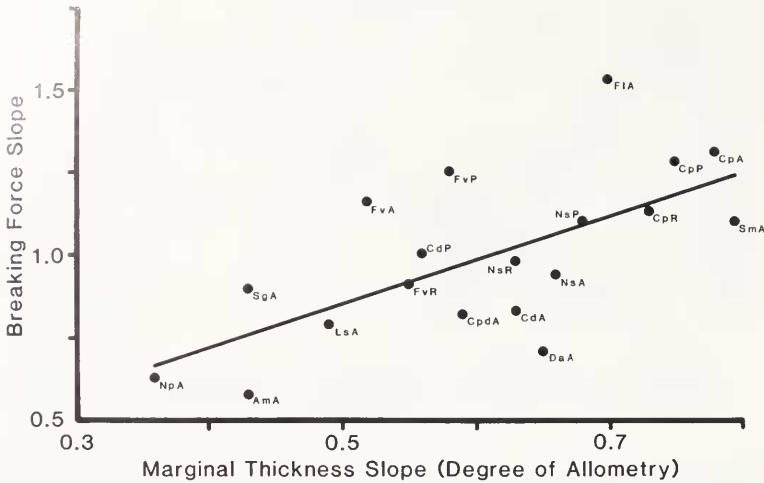


FIGURE 6. Slopes of shell strength ln-ln regressions (SS) versus slopes of marginal thickness ln-ln regressions (MT) for all species and sides of shell. Slopes given as exponents in Tables VI and X. SS represents the rate of increase of shell strength with increasing foot area. MT represents the rate of increase of marginal thickness with increasing foot area (= degree of allometry). SS and MT are positively correlated:  $SS = 0.19 + 1.33MT$ ;  $n = 19$ ;  $r = 0.6589$ ;  $P = 0.0022$ . See Figure 4 for abbreviations.

planar or rounded surfaces. In most cases, the force was applied to opposite sides of whole shells (left and right valves still joined for bivalves) in various orientations across all or much of the entire width of the shell. This kind of "whole-animal" crushing force is generated by certain species of fish (Palmer, 1979) and crabs [when mollusc size/crab size is small (bivalves—Elnor, 1978; Blundon and Kennedy, 1982; Boulding, 1984) (gastropods—Zipser and Vermeij, 1978; Bertness, 1981; Bertness and Cunningham, 1981; Reimchen, 1982; ap Rheinallt and Hughes, 1985; Lawton and Hughes, 1985)].

In contrast, the above studies on crabs have shown that, when the ratio of mollusc size to crab size is large, crabs exhibit a strong tendency to attack the edge of the valve for bivalves or the shell lip, apex, or similar narrow region of the shell for spirally coiled gastropods. These studies have also shown that the probability of an unsuccessful attack is much greater when the ratio of mollusc size to crab size is large. As discussed earlier, this suggests that with respect to crab predation, the potential for selection for the strength of these localized regions of the shell may be greater than for the strength of other regions of the shell. Therefore, measurements of the force required to crush whole shells across the region of greatest width should be used with caution in discussions of the evolution of defensive shell morphologies. In those cases, however, where the thicknesses of different regions of the shell are correlated (as was found for *N. scutum*; Table VIII), such "whole-animal" strengths may be correlated with the strengths of the more critical regions of the shell.

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